

A new species of the genus *Hyalophora* Duncan, 1841 from Central Mexico (Lepidoptera: Saturniidae, Attacini)

WOLFGANG A. NÄSSIG^{1,*}, GUILLERMO NOGUEIRA G.² AND STEFAN NAUMANN³

¹ Entomology II, Research Institute and Natural History Museum Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany.

² c/o Escuela de Biología, Universidad Autónoma de Guadalajara, Av. Patria No. 1201, Lomas del Valle 3ra. Sección, Zapopan, Jalisco, C.P. 44100, México.

³ Hochkirchstrasse 11, D-10829 Berlin, Germany. — Research Associate of Museum für Naturkunde Berlin, Germany.
wolfgang.naessig@senckenberg.de; sn@saturniidae.com

Abstract. A new species of the genus *Hyalophora*, *H. mexicana* sp. n., is described. Specimens from the Mexican Federal States of Zacatecas and Guanajuato as well as male genitalia are illustrated; a distribution map is included. The male holotype is deposited in Colección Nacional de Insectos, Universidad Nacional Autónoma de México, Ciudad México, Mexico. Only male specimens are known so far. The new species is compared with other *Hyalophora* species. The description of the new species is based on studies of imaginal morphology including male genitalia and mtDNA (COI barcode). *H. mexicana* sp. n. is a very large species for the genus, and with its combination of typical characters such as reddish colouration, rounded, drop-shaped ocellular patches of the wings, a reduced, quarter-circle band of blue scales in the subapical ocellus of the forewing and details in male genitalia structures it can be separated easily from all hitherto known northern species. In addition, some taxonomic and nomenclatural problems in *Hyalophora* are addressed.

Key words: *Hyalophora mexicana* sp. n., Zacatecas, Guanajuato, Sierra Madre Occidental.

INTRODUCTION

The genus *Hyalophora* Duncan, 1841 is presently known with three species from the North American continent, especially from north of Mexico. According to recent literature (e.g., Lemaire, 1978; 1996; Tuskes *et al.*, 1996; Collins, 1997; Powell & Opler, 2009), the following three species are known from southern Canada and the United States:

Hyalophora cecropia (Linnaeus, 1758) in the eastern and central area (western limits see Peigler & Opler, 1993; the maps by Peigler & Opler were made before the true nature of *kasloensis* was published and contain misidentifications; their plots for *cecropia* in Utah and Washington are almost certainly errors; Collins, pers. comm.),

H. columbia (Smith, 1865) with two (or three) subspecies, *H. columbia columbia* (and perhaps *H. c. nokomis* (Brodie, 1894)?) in central to eastern Canada and *H. c. gloveri* (Strecker, 1872) in the Rocky Mountains/ Great Basin area; this taxon was listed as a separate fourth species by Ferguson, 1972), with a red “form” in southern Arizona (Ferguson, 1972: 257; Peigler & Opler, 1993; Powell & Opler, 2009: 241); and

H. euryalus (Boisduval, 1855) [= *rubra* Neumoegen & Dyar, 1894] in the West, primarily along the Pacific Coast (Peigler & Opler, 1993; Tuskes *et al.*, 1996), with probably a subspecies on Cedros Island, Baja California, Mexico (see below). Populations in the interior of British Columbia, Canada, and in the Bitterroot Mts. of Idaho and Montana (USA), named as subspecies *kasloensis* Cockerell [*in* Packard, 1914], have usually been treated as a hybrid intergrade between *euryalus* and *gloveri* (Sweadner, 1937; Tuskes *et al.*, 1996; Collins, 1997; 2006), or alternatively as a subspecies of *euryalus* (e.g., Ferguson, 1972).

*83rd Contribution to the Knowledge of the Saturniidae (82nd Contribution see: Naumann, S., S. Löffler & W. A. Nässig. 2012. Revisional notes on the species-group of *Saturnia cachara*, with description of a new subgenus and a new species (Lepidoptera: Saturniidae). — Nachrichten des Entomologischen Vereins Apollo, Frankfurt am Main, N.F. 33 (2/3): 107–128).

Received: 19 November 2013

Accepted: 11 September 2014

Copyright: This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported License. To view a copy of this license, visit <http://creativecommons.org/licenses/by-nc-nd/3.0/> or send a letter to Creative Commons, 171 Second Street, Suite 300, San Francisco, California, 94105, USA.

These three species are closely related, and most authors agree that local hybridisation and introgression occurs in areas where they meet naturally (Tuskes *et al.*, 1996; Collins, 1997; 2007; Collins & Rawlins, 2014). Apparently *H. columbia/gloveri* and *H. euryalus* hybridize everywhere they are sympatric or parapatric (Collins, 1984; 1997). Nominotypical *H. columbia* and *gloveri* appear to intergrade completely across Canada (Collins, 1984; Kohalmi & Moens, 1975; 1988). Only *H. cecropia* apparently maintains integrity in sympatry with congeners (Collins, pers. comm.). Earlier observations that at some other places the distribution areas may possibly overlap without regular hybridisation (e.g., Tuttle, 1985; Tuskes *et al.*, 1996) have not found support. In the laboratory obviously all populations can readily be hybridised, but often with at least partially reduced fertility of the hybrid offspring (Tuskes *et al.*, 1996; Collins, 1997). In the wild, a possible hybrid offspring of presently local, isolated populations caused by climate fluctuations and resulting distribution area shifts during especially the ice ages, in which two taxa came into contact only temporarily, may be obscured, and only sometimes can be demonstrated by introgression (Collins, pers. comm.). Further, there are small, but apparently stable differences in male genitalia morphology (Ferguson, 1972; Lemaire, 1978), besides obvious differences in external adult and preimaginal morphology (e.g., Tuskes *et al.*, 1996; Lampe, 2010).

Published records of *Hyalophora* for Mexico are sparse and mostly cover the northern states of Mexico bordering the U.S. only (Fig. 1):

H. euryalus in Baja California Norte, including Cedros Island on the Pacific side of the Baja California peninsula. A separate subspecies was described from this island: *cedrosensis* Cockerell [*in* Packard], 1914; this is — according to literature — the southernmost population of *H. euryalus* (Hoffmann, 1942; Ferguson, 1972; Lemaire, 1978; Smith & Wells, 1993; Tuskes *et al.*, 1996; Powell & Opler, 2009). Material from Baja California and Cedros Island was not accessible to us for this study.

A large reddish form occurs in the northern Mexican federal states of Chihuahua and Sonora (Peigler, 1994; Tuskes *et al.*, 1996) close to the US border, and also in Durango and “to an undetermined distance south” (Tuskes *et al.*, 1996: 208) within the Sierra Madre Occidental, always interpreted as belonging to *H. columbia gloveri*, according to Tuskes *et al.* (1996).

Beutelsbacher-Baigts & Balcázar-Lara (1994: 19) speculated that *H. cecropia* might live in the north of the state of Tamaulipas close to the Texas border, but no record was provided.

Published records from further south in Mexico are even rarer and appear to be somewhat questionable: Hoffmann (1942) reported “*Platysamia cecropia*” from Veracruz state (near Jalapa; recent spelling: Xalapa), but interpreted it as an introduced population; however, Tuskes *et al.* (1996) suspected that this record may also refer to what they call an “especially large, reddish form of *gloveri*.” We have not seen any specimen from Veracruz so far. The specimen cited by Hoffmann (1942) has not been located in his collection today deposited in Ciudad México (Colección Nacional de Insectos, Universidad Nacional Autónoma de México) during a search by one of the authors (G.N.G.). *H. cecropia* is exclusively associated with temperate North American open woodland and meadows, especially somewhat disturbed areas (even city suburbs); apparently, it reaches its warm climate tolerance near San Antonio (Texas) (Collins, pers. comm.). However, Ferguson (1972: 247) also listed it from Brownsville (Texas) at the Rio Grande borderline between the USA and Mexico. So, if it is not just a misidentification of a population of “*H. gloveri sensu lato*” (Tuskes *et al.* 1996) or the result of an artificial introduction of *H. cecropia* as indicated by Hoffmann (1942), it may alternatively reflect a formerly continuous distribution of *H. cecropia* through the lowlands and lower slopes of the Sierra Madre Oriental along the Caribbean (eastern) coastline of Mexico. Brownsville in Texas at the Rio Grande is, in a bent line along the Caribbean coastline, approximately 750 km from Xalapa in Veracruz state, and a much smaller distance from Tamaulipas (Beutelsbacher-Baigts & Balcázar-Lara, 1994, but see above).

Specimens found in the Sierra Madre Occidental range in the Mexican federal states of Guanajuato and Zacatecas by one of the authors (G.N.G.) between 1997 and 2013 gave us the chance to study these apparently rare Central Mexican moths in more detail. A few further specimens of this population were found by G.N.G. and Jean Haxaire, also in Zacatecas (now in collections D. Herbin and R. Rougerie). Every colleague with whom we discussed these findings in early times of our study expected (pers. comm.), according to Tuskes *et al.* (1996), that the Central Mexican red *Hyalophora* would be southern outliers of those northern red populations in Arizona and northern Mexico (Sonora, Chihuahua, Durango).

The mtDNA barcodes of several of these Guanajuato and Zacatecas specimens were analysed. During our study we compared our data with other *Hyalophora* barcodes, either of our own material or in public records in BOLD, and also with further data through support by Rodolphe Rougerie as well as Michael M. Collins, Jim Fetzner and John Rawlins



Figure 1. Distribution of *Hyalophora mexicana* and related species of *Hyalophora* in Mexico and bordering states of the USA (species code see insertion). One dot may represent more than one locality if in close proximity; we have not located every label or published data on the map. Many more or less inexact records of (usually) "*H. columbia gloveri*" from northern Mexico and southern USA in general literature have not been included or (when exact locality data was available) are represented as white dots, as they have not been identified by barcode. — Map created with Map Creator 2.0 Personal Edition, © 2003–2007 primap software, modified and localities added (W.A.N.).

(Carnegie Museum of Natural History, Pittsburgh, PA). In spite of the fact that there still are some uncertainties (mainly due to lack of data) about several of the northern taxa and populations of *Hyalophora*, we decided to describe this southernmost, now relatively well-characterised population from Guanajuato and Zacatecas here according to the results of this study as a new species of the genus, based on external and genitalia morphology and sequence data of part of the mitochondrial COI gene.

There are still taxonomic problems. Apparently not every population in the USA which presently is called "*Hyalophora columbia gloveri*" truly represents that species (respectively, subspecies), based on our present knowledge. A paratype of the new species will be deposited in the Carnegie Museum to allow American colleagues access to the new species.

MATERIALS AND METHODS

We used all *Hyalophora* specimens available to us in the collections of Senckenberg Frankfurt (SMFL), coll. S. Naumann, Berlin, and, for the new species, all specimens collected by G.N.G. and later dispersed to the collections shown in the types list. Morphological studies on imagoes followed standard procedures; photos of the set specimens were taken with a digital camera and a circular daylight fluorescent tube. The last segments of the abdomen of male moths were cut off and macerated in ca. 2–3% aqueous NaOH solution at ca. 96–98°C for 1 h to clean the genitalia from scales, fat and tissue. After dissection in water and low-concentrated ethanol, the genitalia were stored in 70% ethanol in vials. The drawings were produced from "unflattened" genitalia in ethanol;

we believe, in accordance with, e.g., Zwick (2009: 148), that the preservation of the undistorted three-dimensional structure of the genitalia is essential for the understanding of their function. The genitalia photograph was taken from a flattened, slide-mounted preparation.

Data of the specimens which were used for the mtDNA analysis are listed in Table 1. The so-called COI barcode is based on the sequence data of a short 658 base pairs region of the mitochondrial cytochrome-*c*-oxidase, subunit I [COI], gene. DNA was extracted from the legs of dried specimens mainly in the collections of the authors. Further sequence data kindly provided by Michael M. Collins, Jim Fetzner and John Rawlins were used for comparison. Technical details and references relative to the laboratory protocols see in Ratnasingham & Hebert (2007), on the CCDB website (CCDB 2014) and also in, e.g., Decaëns & Rougerie (2008) or Vaglia *et al.* (2008). Sequences of the specimens analysed are deposited in GenBank (Table 1). The analysis of sequence data was conducted using MEGA5 (Tamura *et al.*, 2011); see Fig. 2.

We used one specimen each of the three species of the genus *Callosamia* as outgroup to root the mtDNA barcode trees. *Callosamia* generally most often shows up as North American sistergroup of *Hyalophora* in COI barcode trees, irrespective which analysis method is used.

The COI barcode data of 37 *Hyalophora* plus the 3 *Callosamia* specimens used in our analysis were generated either in Guelph, Ontario, by Bold (2014) or provided by Jim Fetzner, John Rawlins and Michael M. Collins. We used only sequences that were more than 600 base pairs (bp) long. Shorter sequences as well as those from specimens of doubtful origin were discarded.

Abbreviations used

BC — Barcode [no.].

CDHP — Collection Daniel Herbin, Pechabou, France.

CGNG — Collection Guillermo Nogueira G., Zapopan, Jalisco, México.

CMNH — Carnegie Museum of Natural History, Pittsburgh, PA, USA.

INBUNAM — Instituto de Biología (Colección Nacional de Insectos), Universidad Nacional Autónoma de México, Ciudad México (Mexico City), Mexico.

CRRR — Collection Rodolphe Rougerie, Rouen, France.

CSNB — Collection Stefan Naumann, Berlin, Germany.

SMFL — Senckenberg-Museum, Lepidoptera collection, Frankfurt am Main, Germany (including coll. W. A. Nässig).

UAG — Universidad Autónoma de Guadalajara collection, Zapopan, Jalisco, México.

RESULTS

Based on our results, we here describe the “big red species” of *Hyalophora* from Central Mexico (Mexican Federal States of Zacatecas and Guanajuato) as a new species:

Hyalophora mexicana sp. n.

Holotype ♂: Mexico, Zacatecas, La Manchada, 1966 m, 28. vii. 2003, dissection number WAN 1988/07, barcode B3218-wn-B08, leg. G.N.G. Deposited in the INBUNAM collection at the Universidad Nacional Autónoma de México in Mexico City, Mexico. Figs. 3a–3b.

Paratypes (in total 10 ♂♂), all Mexico (see Fig. 1, map):

Guanajuato (3 ♂♂): 1 ♂, Sierra de Santa Rosa, 2300 m, 2.–3. vii. 1997, leg. G.N.G., Barcode B3218-wn-B07, SMFL (Figs. 4a–4b). 1 ♂, Sierra de Santa Rosa, 2634 m, 8. vii. 2013, leg. G.N.G., CGNG. 1 ♂, Sierra de Santa Rosa, 2347 m, 9. vii. 2013, leg. G.N.G., CSNB.

Zacatecas (7 ♂♂): 1 ♂, Florencia de B.J., 2114 m, 26. vii. 2003, leg. G.N.G., SMFL. 2 ♂♂, Tlaltenango de Sánchez, 2591 m, 27. vii. 2003, leg. G.N.G., barcode SNB 1686 (this specimen in CSNB, the other specimen will be deposited in CMNH). 1 ♂, La Manchada, 1966 m, 28. vii. 2003, dissection number WAN 1965/05, barcode B3218-wn-B09, UAG. 1 ♂, La Manchada, Momax, 1950 m, 21°57'54" N, 103°12'20" W, 17. vi. 2009, SMFL. — 1 ♂, Zacatecas, ‘dirt road’ Momax to San Lorenzo, behind San Lorenzo, 2 km toward La Manchada, 1935 m, 30. vii. 2003, leg. G.N.G., J. Haxaire & O. Paquit, BC-Roug1230, CRRR. 1 ♂, Zacatecas, same data, but 28. vii. 2003, BC-Her2360, CDHP.

Etymology: named after the country of origin, Mexico.

DESCRIPTION AND DIAGNOSIS

♂: Generally, a large species in the genus, with the holotype in most measurements being the largest and the specimens from Guanajuato on average the smallest.

As given in detail below, it is unique in the genus by the combination of its reddish-brown ground colour; the quite rounded, drop-shaped ocellular patches of both fore- and hindwings; a typical blue marking of the forewing subapical ocellus; broad and relatively straight, not undulate postmedian lines; and in male genitalia the extended sacculus and the typical spine of the vesica.

Measurements: Holotype: forewing: length (fwl., measured from base to tip of apex) [all wing measurements of left side of holotype] 7.8 cm, forewing (fw.) eyespot or discoidal patch largest diameter (l.d.) 1.3 cm, apical spot l.d. 0.86 cm; hindwing length (hwl.) 5.6 cm, hw. eyespot l.d. 1.4 cm. Antenna ca. 20.3 mm long, longest rami ca. 4.0 mm long. — All males (holotype and available paratypes together, $n = 7$ except see below): fwl. 6.4–7.8 cm, average 6.89 cm $\pm$ 0.46 s.d.; fw. eyespot l.d. 1.1–1.3 cm, average 1.19 cm $\pm$ 0.08 s.d.; apical spot l.d. 0.60–0.86 cm, average 0.67 $\pm$ 0.08 s.d.; hindwing length (hwl.) 4.7–5.6 cm, average 5.17 cm $\pm$ 0.29 s.d.; hw. eyespot

Table 1. Data of the specimens of *Hyalophora* (37 specimens) and *Callosamia* (3 specimens, included as outgroup) used for the mtDNA sequence analysis. — Additional abbreviations: GBAC = GenBank Access Code; HT = holotype; PT = paratype; SL = Sequence Length (data from BOLD or simple count of bp); — = information not available. — In the same order of taxa and specimens as in the tree graph, Fig. 2.

Species	Sample-ID	Process-ID	GBAC	SL	Deposition	Locality of Origin
<i>H. gloveri</i> “a”	SNB 1699	SASNB699-09	GU702999	658[0n]bp	CSNB	USA, Arizona, Cochise Co., Guadalupe Canyon
<i>H. gloveri</i> “a”	SNB 1863	SASNB768-10	HQ579817	658[0n]bp	CSNB	USA, Arizona, Cochise Co., Guadalupe Canyon
<i>H. gloveri</i> “a”	MGS 734	—	KJ865746	658 bp	CMNH	USA, Arizona, Cochise Co., Huachuca Mtns.
<i>H. gloveri</i> “a”	MGS 723	—	KJ865745	658 bp	CMNH	USA, Arizona, Cochise Co., Huachuca Mtns.
<i>H. gloveri</i> “a”	MGS 721	—	KJ865744	658 bp	CMNH	USA, Arizona, Cochise Co., Huachuca Mtns.
<i>H. gloveri</i> “a”	MGS 707	—	KJ865743	658 bp	CMNH	USA, Arizona, Graham Co., Pinaleno Mtns.
<i>H. gloveri</i> “a”	MGS 569 = 570	—	KJ865742	658 bp	CMNH	USA, Arizona, Hualapai
<i>H. gloveri</i> “a”	MGS 233	—	KJ865741	658 bp	CMNH	USA, Arizona, Gila Co., Payson
<i>H. columbia</i> (grey like <i>gloveri</i>)	SNB 1861	SASNB766-10	KM287184	658[0n]bp	CSNB	USA, Colorado, Colorado Springs
<i>H. columbia</i> (blackish)	B3218-wn-C05	SAWNA027-09	GU703464	658[0n]bp	SMFL	Canada, Ontario, Norland
<i>H. columbia</i> (blackish)	B3218-wn-C06	SAWNA028-09	GU703465	658[0n]bp	SMFL	Canada, Ontario, Norland
<i>H. columbia</i> (grey like <i>gloveri</i>)	SNB 1860	SASNB765-10	HQ579815	658[0n]bp	CSNB	USA, Colorado, Colorado Springs
<i>H. columbia</i>	SNB 1698	SASNB698-09	HM383529	658[0n]bp	CSNB	Canada, Ontario, Haliburton Highlands
<i>H. columbia</i>	SNB 1857	SASNB762-10	HQ579814	658[0n]bp	CSNB	Canada, Ontario
<i>H. columbia</i> (hybr. with <i>cecropia</i> ?)	SNB 1866	SASNB771-10	HQ579818	658[1n]bp	CSNB	Canada, Ontario, Haliburton Highlands
<i>H. cecropia</i>	SNB 3227	SASNC1238-11	KM287185	658[0n]bp	CSNB	USA, New Jersey, Beachwood
<i>H. cecropia</i>	SNB 1869	SASNB774-10	HQ579819	658[0n]bp	CSNB	USA, Texas, Bexar Co., San Antonio
<i>H. cecropia</i>	SNB 3237	SASNC1248-11	KM287195	658[0n]bp	CSNB	USA, Wisconsin, Portage Co.
<i>H. columbia nokomis</i> (hybr. with <i>cecropia</i> ?)	SNB 1859	SASNB764-10	KM287192	658[0n]bp	CSNB	Canada, Ontario, Mafeking
<i>H. cecropia</i>	B3218-wn-B11	SAWNA022-09	GU703463	658[0n]bp	SMFL	Canada
<i>H. cecropia</i>	SNB 3228	SASNC1239-11	KM287183	658[0n]bp	CSNB	USA, New Jersey, Beachwood
<i>H. cecropia</i>	SNB 1867	SASNB772-10	KM287193	658[0n]bp	CSNB	Canada, Ontario, Haliburton Highlands
<i>H. cecropia</i>	SNB 1871	SASNB776-10	KM287190	658[0n]bp	CSNB	USA, Colorado, Denver
<i>H. euryalus</i>	B3218-wn-C02	SAWNA024-09	GU703536	658[0n]bp	SMFL	USA, California, Monterey
<i>H. euryalus</i>	SNB 1694	SASNB694-09	GU703001	658[0n]bp	CSNB	USA, California, San Diego, vic. Escondido
<i>H. euryalus</i>	B3218-wn-C01	SAWNA023-09	GU703535	658[0n]bp	SMFL	USA, Washington, Chelan Co., vic. Leavenworth
<i>H. euryalus hasloensis</i>	SNB 1696	SASNB696-09	GU703000	658[0n]bp	CSNB	Canada, Brit. Columbia, Okanagan Valley
<i>H. euryalus</i>	SNB 1695	SASNB695-09	GU703002	658[0n]bp	CSNB	USA, California, Nevada Co.
<i>H. euryalus</i>	SNB 1858	SASNB763-10	KM287188	658[0n]bp	CSNB	USA, California, Nevada Co.
<i>H. gloveri</i> “b”	B3218-wn-C03	SAWNA025-09	GU703533	658[0n]bp	SMFL	USA, Utah, Box Elder Co.
<i>H. gloveri</i> “b”	B3218-wn-C04	SAWNA026-09	GU703534	658[0n]bp	SMFL	USA, [reared, no data]
<i>H. gloveri</i> “b”	SNB 1864	SASNB769-10	KM287189	658[0n]bp	CSNB	USA, Utah
<i>H. mexicana</i> PT	SNB 1686	SASNB686-09	GU703009	658[0n]bp	CSNB	Mexico, Zacatecas, Tlaltenango de Sánchez
<i>H. mexicana</i> PT	B3218-wn-B07	SAWNA018-09	GU703460	658[0n]bp	SMFL	Mexico, Guanajuato, Sierra de Santa Rosa
<i>H. mexicana</i> HT	B3218-wn-B08	SAWNA019-09	GU703461	658[0n]bp	SMFL	Mexico, Zacatecas, La Manchada
<i>H. mexicana</i> PT	B3218-wn-B09	SAWNA020-09	GU703462	658[0n]bp	SMFL	Mexico, Zacatecas, La Manchada
<i>H. mexicana</i> PT	BC-Roug1230	SATWB181-11	KM287191	633[0n]bp	CRRR	Mexico, Zacatecas, ‘dirt road’ Momax to San Lorenzo, after San Lorenzo
<i>C. promethea</i>	SNB 1856	SASNB761-10	HQ579813	658[0n]bp	CSNB	Canada, Quebec
<i>C. angulifera</i>	SNB 1853	SASNB758-10	HQ579812	658[0n]bp	CSNB	USA, Pennsylvania
<i>C. securifera</i>	SNB 1852	SASNB757-10	KM287187	633[1n]bp	CSNB	USA, Florida, Lake Co.

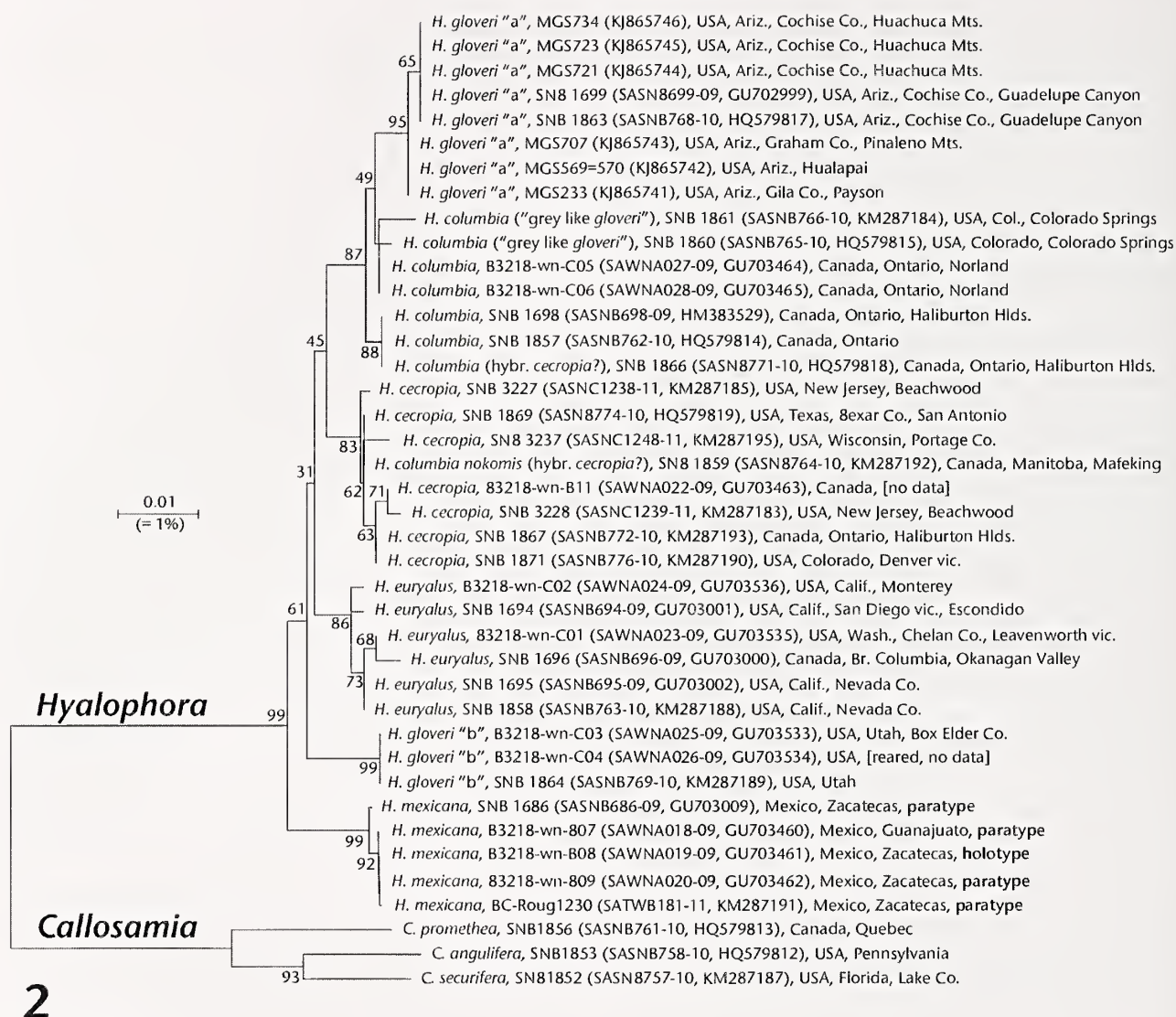


Figure 2. The tree of *Hyalophora* taxa was inferred using the Neighbour-Joining method (Saitou & Nei, 1987). The optimal tree with the sum of branch length = 0.19203706 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (3000 replicates) are shown next to the branches (Felsenstein, 1985). Evolutionary distances were computed using the Maximum Composite Likelihood method (Tamura *et al.*, 2004). The rate variation among sites was modeled with a gamma distribution (shape parameter = 3). The differences in the composition bias among sequences were considered in evolutionary comparisons (Tamura & Kumar, 2004). The analysis involved 40 nucleotide sequences (= specimens). There were a total of 653 positions in the final dataset. Analyses were conducted in MEGA5 (Tamura *et al.*, 2011).

l.d. 1.0–1.5 cm, average 1.29 ± 0.14 s.d. Antenna with ca. 33–34 segments ($n = 2$), quadripectinate to their tip; ca. 17–21 mm long ($n = 7$, average $19.19 \text{ mm} \pm 0.13$ s.d.), longest rami ca. 3.5–4.0 mm ($n = 7$, average $3.79 \text{ mm} \pm 0.21$ s.d.).

Colour and wing pattern: Ground colour on dorsal side intensive reddish brown; colour tone similar to *H. euryalus*. Antennae very dark brown to mostly black (in the similar *H. euryalus* dark brown). Head, dorsal parts of thorax and abdomen in ground colour,

between head and thorax a wide white collar, thorax and abdomen separated by a white band of long hair, abdomen with intersegmental white stripes.

Forewing in ground colour, with broad white antemedian and little bent postmedian line, both bordered black to median area, nearly straight and not dentate, white middle part widening to the anal margin. The forewing ocellular patch more or less rounded, drop-shaped, with its tip directed to the outer margin, white, with yellow, orange and black

outer border. Postmedian area again in ground colour, in the marginal parts suffused with ochreous scales, then becoming completely ochreous. Marginal area separated from the postmedian area by a thin black line with rounded indentions between the veins, of light ochreous-white colour with around 2 mm broad darker outer margin (in most of the northern taxa, especially in the generally similar *H. euryalus*, this median area is darker greyish, not differing in tone from outer postmedian area). The apical postmedian area with a violet and pink dash, and an outer small white zigzag line. The round subapical ocellus intensive black with some blue scales in shape of a quarter circle in the top and inner quadrant of the subapical ocellus (in most specimens of the other taxa this bluish “eye shadow” forms a full lunule in the inner half of the ocellus).

Hindwing of same colouration as forewing, but basal/antemedian area whitish, without red. The hindwing discoidal patch a somehow drop-like widened lunule, with its tip directed to the outer margin. Along the white postmedian line on outer side the inner portion (for about 1 mm) of the postmedian area only with red, not interspersed with grey or black scales, somehow resembling *H. cecropia* in this aspect (in other taxa, the grey to black scales are interspersed just to the white postmedian), but without orange colour tone. The ochreous part of the postmedian area shows a row of grey patches (in most other taxa darker grey or black). On ventral side with almost same ornamentation, but of much darker colour, much less red. Thorax with legs and the abdomen in ground colour. Both fore- and hindwings are strongly suffused with black and white scales, and only the marginal postmedian area and the marginal area are of same colour as on upperside. The antemedian line is completely missing on all wings, and the hindwing has a broad white upper margin. The underside is somewhat similar to *H. euryalus*; other species with much less red on underside, mostly grey.

♂ **genitalia** (Fig. 6, Fig. 7; Figs. 8–10 for comparison with several other *Hyalophora* taxa): Uncus bifid with two long rounded tips, curved to ventral side. Valves of *Hyalophora* are generally quite globularly in shape and impossible to be flattened without distortion for photographing. Dorsal process of the valves somewhat rounded, bent to inner side, the ventral one small, slender, and with a ventrally pointing tip. The sacculus is well developed, with rounded tip, and larger than in any other *Hyalophora* species. Gnathos narrowing to tip, sometimes with a little indentation (in other species always broader to tip, more plate-like), juxta with two lateral short symmetrical triangular

processes, slightly shorter than in other taxa. Saccus large and rounded. Phallus straight, sclerotised part ca. 4.8–5 mm long, vesica with a dorsal projection with sclerotised thorn, a thorn-like unsclerotised ventral projection, and a distal longer bulb.

♀, **preimaginal instars, ecology and larval foodplants** unknown.

General information on and description of some of the collecting localities and methods

Zacatecas, La Manchada: Elevation 1966 m, 21°57' N, 103°12' W; 28. VII. 2003; 1950 m, 21°58' N, 103°12' W, 17. VII. 2009, Momax. The area in Zacatecas where most of the *Hyalophora* specimens were collected is found at the “Region Mezoamericana de Montaña” in the “Province of the Sierra Madre Occidental” (Rzedowski, 1994), with sedimentary and volcano-sedimentary rocks from the Cenozoic Era (INEGI 1981) with a moderately acidic soil. A locality is found in a small canyon that runs down from E to W from the Sierra Morones. The climate classification at the area according to Garcia (1973) is “Acwo (semicalido y subhumedo).” The area has about 700–1000 mm annual rainfall, 60–65% of average relative humidity and an annual mean temperature range of 18–22° C (Llorente *et al.*, 1996). At the collecting site we found a *Quercus* forest (Fig. 11), mixed with some other vegetation elements. Plant species in the forest vegetation recorded for this area included: *Quercus chihuahuensis* (Trel.), *Qu. eduardii* (Trel.), *Qu. magnoliifolia* (Née) (Fagaceae), some *Pinus oocarpa* (Schiede), *P. michoacana* (Martínez) (Pinaceae), some other vegetation elements from lower and higher altitude range present at this site are *Acacia schaffneri* (S. Watson), *A. farnesiana* (L.) Willd., *Prosopis* spp., *Mimosa* spp., *Mimosa biuncifera* (Benth.) (Fabaceae), *Larrea* spp. (Zygophyllaceae), *Baccharis* spp. (Asteraceae), *Opuntia* spp. (Cactaceae), *Arbutus arizonica* (Gray) Sarg. (Ericaceae) (Rzedowsky 1994, Vazquez-Garcia *et al.* 2004). The ♂♂ of *Hyalophora mexicana* n. sp. arrived to lights between 21:30 h and 0:30 h, after this time the weather often became very windy. Nevertheless we continued light-trapping until 3:00 h or later, waiting for a ♀, but none appeared. These activity times are slightly in contrast to the observations by Collins (2007: 69) on *Hyalophora* males arriving at light around 4:00 h.

Guanajuato, Sierra de Santa Rosa: Elevation 2300 m, 21°5' N, 101°12' W; 2.–3. VII. 1997. This locality which provided our first record for the new *Hyalophora* is found in the “Region Xerofítica Mexicana” in the “Province of the Altiplanicie” (Rzedowski, 1994), with extensive igneous rocks of the Cenozoic Era (INEGI 1981) with moderately acidic

soils. The locality is found in a canyon that runs down from SE to NW. The climate classification at the area according to García (1973) is "Acwo (semicalido y subhumedo)." The area has about 700–1200 mm annual rainfall, 60–65% of average relative humidity and an annual mean temperature range of 18–22° C (Llorente *et al.*, 1996). At the collecting site we found a *Quercus* forest, mixed with some other elements. Plant species in the forest vegetation recorded for this area at higher altitudes included *Pinus oocarpa* (Schiede), *P. michoacana* (Martínez) (Pinaceae), at the collecting site we found *Quercus crassifolia* (Humb. & Bonpl.), *Quercus mexicana* (Humb. & Bonpl.), *Qu. jaralensis* (Trel.), *Qu. castanea* (Née), *Qu. rugosa* (Née) (Fagaceae); some other elements are *Salix* spp., *Populus* spp. (Salicaceae), *Fraxinus* spp. (Oleaceae), *Cercocarpus* spp. (Rosaceae) (Rzedowsky 1994, Zavala 2003). The first ♂ found at this locality arrived to the lights between 22:30 h and 23:30 h.

Collecting methods in all localities: Regularly two different sets of lights were operated in parallel by G.N.G. who collected most of the specimens known. For one set of lights two white sheets were used, one in vertical position and the second on the floor; one 20 W UV light tube with filter ("superactinic light"), one 20 W UV light tube without filter ("blacklight"), two 15 W UV tubes with filter and a 150 W Mercury vapor bulb with white and UV light, all powered by a generator. For the second set of lights, again two small white sheets were used, one placed on the floor and the second at ca. 80 cm above on a tripod. This set was placed in the forest approx. 100 m away from the first set (powered by the generator or by a battery) and consisted only of originally two (later three) 20 W UV light tubes, one with filter and the other one(s) without filter. This smaller set of UV tubes is internally called the "ghost", because it looks very strange at dark night in the wild from some distance. Regularly the collecting time started at the beginning of the night and ended at sunrise. Most of the *Hyalophora* specimens arrived at this smaller set; the 2009 specimens at the larger equipment with (at that time) 3 tubes.

Potential larval hostplants: Preimaginals are thus far unknown. Known hostplants for other *Hyalophora* species in the wild (south of Canada) usually comprise members of Rosaceae, Ericaceae and Rhamnaceae families (besides a few others). With respect to the Sierra de Santa Rosa, Martínez-Cruz *et al.* (2009) list *Rosa* spp. (Rosaceae), *Ceanothus coeruleus* (Lag.)

(Rhamnaceae) and, quite common, *Arbutus glandulosa* (Mart. & Gal.) (Ericaceae) to be found in this area. In fact, at least one bush of *Ceanothus coeruleus* was very close to the "ghost" light collecting site in the Sierra de Santa Rosa. So, potential standard foodplants of the genus appear to be well available in the area.

DISCUSSION

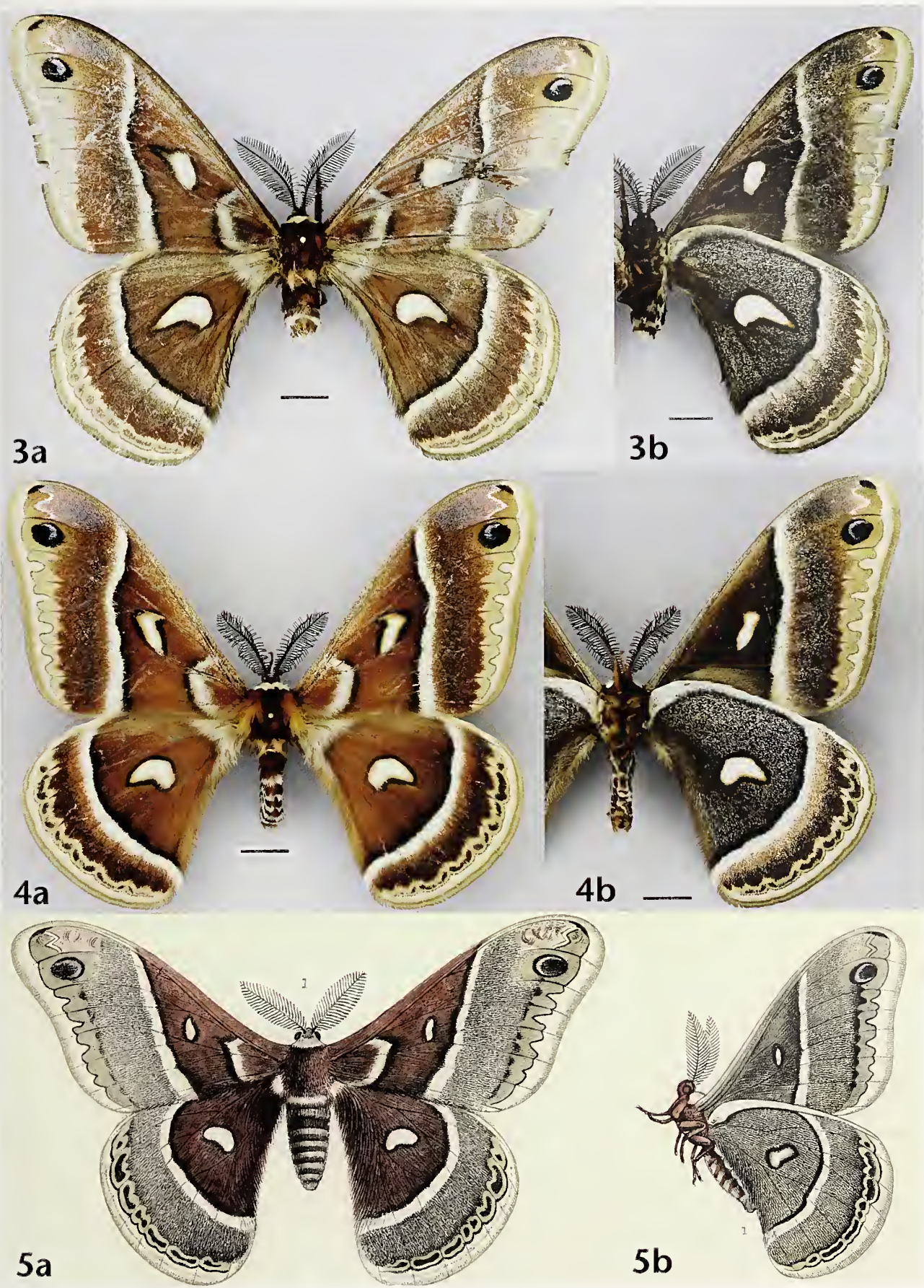
Definition and distribution of the new species *H. mexicana*

An interesting result of our study was that the red "gloveri" from southeastern Arizona and northern parts of Mexico close to the US border is specifically distinct from the red Central Mexican *H. mexicana* sp. n. (and possibly also from other, usually more greyish "gloveri" populations from USA). This result was in contrast to interpretations and predictions by earlier authors and colleagues.

Presently we do not know much about geographical distinction and ecological differences between the complex of "*H. c. gloveri* sensu lato" and the new species *H. mexicana* within Mexico and especially the Sierra Madre Occidental range. The northern and central parts of Mexico and of the Sierra Madre Occidental range are mostly dry and desert-like (e.g., the large Sonora Desert). We suppose that the populations in the southern Sierra Madre Occidental range (in Zacatecas, Guanajuato and possibly elsewhere?) are presently rather well isolated from the northeastern populations (i.e. those from localities in Coahuila and Nuevo León in the Sierra Madre Oriental, see map), as well as from the northwestern populations (i.e. those from the localities in northern Durango, Sonora and Chihuahua). These northwestern populations indeed appear to be southern outliers of the different "*gloveri sensu lato*" populations of New Mexico, Arizona, and western Texas (Tuskes *et al.*, 1996) or separate populations (or "haplotype groups") with more or less differentiated gene pools.

Morphological differences between the long accepted three (or more) northern species of the genus *Hyalophora* are easily visible, mainly in the different colouration of the involved species; differences in male genitalia are generally minor and mainly based on the form of the processes of the uncus, the ventral process of the valves, the sacculus, and the size and number of spines on the vesica. The here described *H. mexicana* has almost the same reddish-brown

Figures 3–5 (Opposite page). Specimens of *Hyalophora*; a = uppersides, b = undersides. **3.** *H. mexicana*, holotype ♂. **4.** *H. mexicana*, paratype ♂, Guanajuato. Scale bars = 1 cm. **5.** *Platysamia gloveri* Strecker, 1872, ♂ syntype; copied from Strecker's (1872) plate, fig. 1. No scale.



ground colour as *H. euryalus*, but is larger than this species and has more rounded, somewhat drop-like discoidal patches. *H. columbia* s.l., when reddish in ground colour at all, shows a more purple, carmine or darker blackish colour. *H. cecropia* has a typical orangy red colour element in the postmedian fascia which is not shared by any other taxon except (but there without any orange tone) in *H. mexicana*. In ♂ genitalia the two sclerotised spine-like projections of the vesica are only shared with *H. columbia* s.l., and the somewhat prominent sacculus is also found, clearly less pronounced, in *H. euryalus*.

COI barcode data

Not unexpectedly, the taxa of the genus *Hyalophora* appear to be closely related, and their speciation process is obviously rather recent and perhaps not yet “finished” in all cases. They are clearly “good” species in terms of wing pattern, immature characters, ecology, and geographic distribution (Collins, pers. comm.). The differences in the barcode sequences are rather low (Fig. 2 and Table 2), but the percentage of difference is (for the specimens of *Hyalophora* calculated) highest for *H. mexicana* sp. n. versus all other *Hyalophora* (between 2.2 and 2.6%, compared with the other taxon groups, see Table 2). *H. mexicana* sequences formed a distinct basal cluster relative to all other *Hyalophora* studied, with high bootstrap support (99%). Of the other *Hyalophora*, only *H. “gloveri” b*, at the second branching, has a comparable sequence distance (between 1.6 and 2.3% versus all other *Hyalophora* except *H. mexicana* sp. n.) and equal bootstrap support. For all other comparisons between populations, distance values are below 2%. Also their bootstrap values are generally low, sometimes even below 50%; only *H. “gloveri” b*, *H. “gloveri” a* and *H. mexicana* sp. n. show support values above 90% (Fig. 2).

Rather low barcode differences are generally not very rare in the family Saturniidae (e.g., Nässig *et al.*, 2010; Naumann & Löffler, 2013). Often times, other characters (morphological, geographical or ecological evidence etc., but also including biological effects like reduced hybrid fertility) must additionally be taken into account to define species limits. Recent speciation does not necessarily require clear differences in all characters.

CONCLUSIONS

We cannot agree with Tuskes *et al.* (1996) who interpreted these Mexican *Hyalophora* as being conspecific with *H. columbia gloveri* (sensu lato); the differences between *H. mexicana* n. sp. and any of the other species are larger than those between any other of

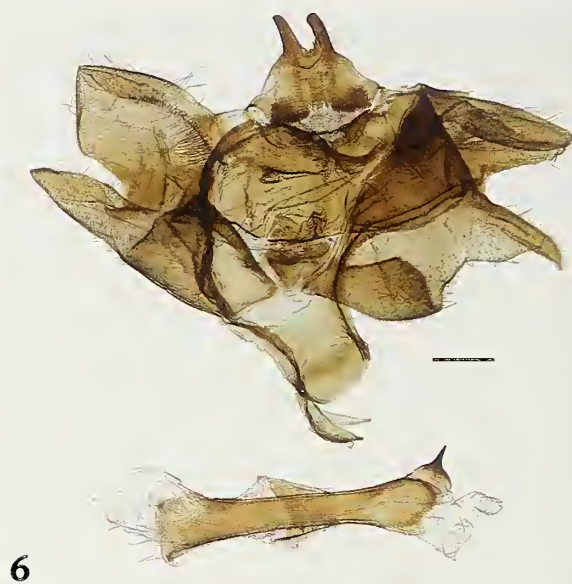


Figure 6. Photo of ♂ genitalia, *Hyalophora mexicana* sp. n., holotype, GP no. WAN 1988/07, barcode B3218-wn-B08, in INBUNAM. Scale bar = 1 mm.

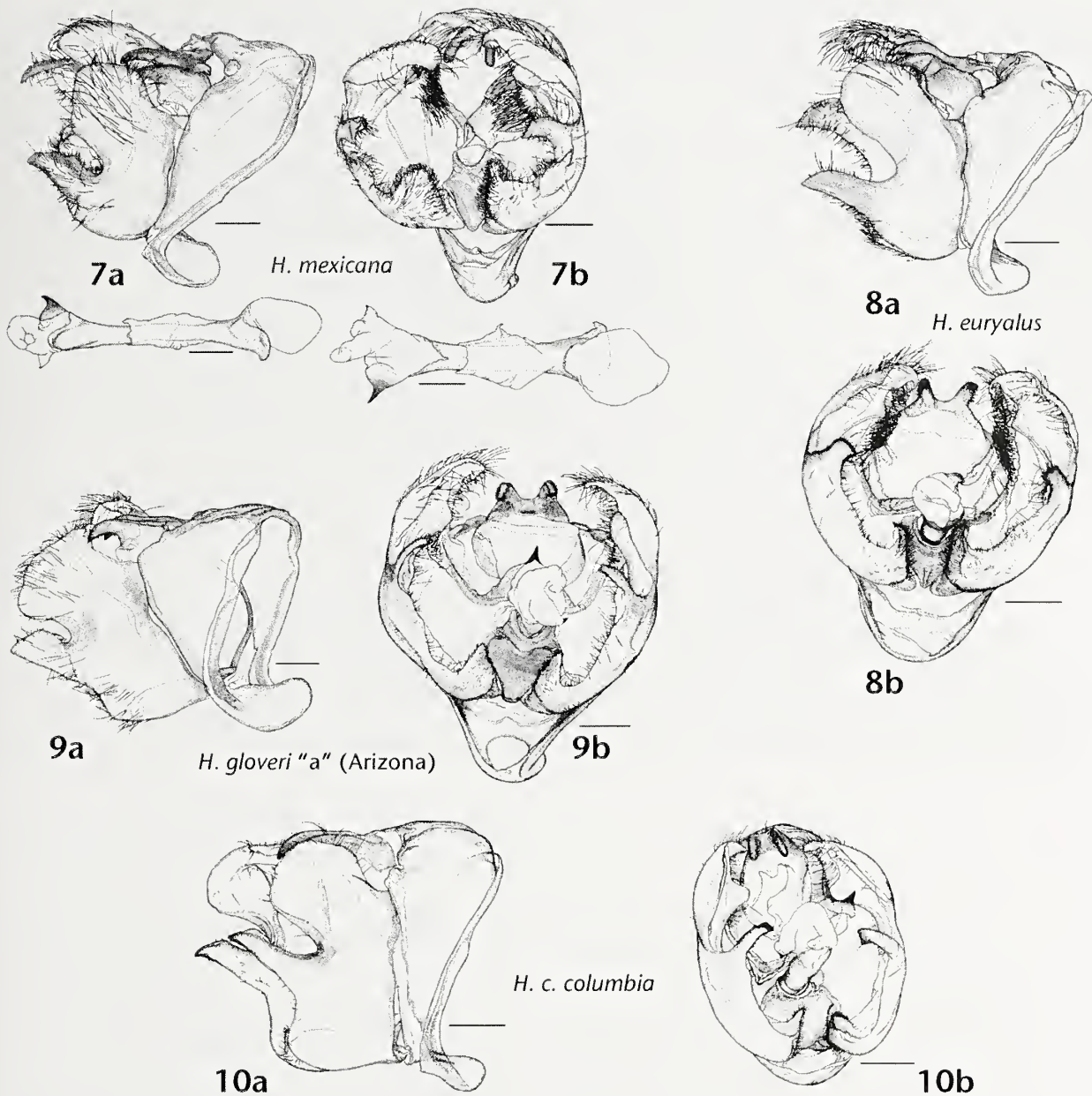
the presently accepted northern species of *Hyalophora*. The new species *H. mexicana* from Central Mexico does neither show all the characters of *H. columbia gloveri*, nor is it evidently the sister-taxon of that complex, in contrast to the opinion of Tuskes *et al.* (1996).

H. mexicana, in spite of its similar colouration, is also clearly not conspecific with *H. euryalus* from the Pacific coastline. Possibly *H. mexicana* is a basal offshoot of the genus, at least when interpreting the barcode results in a phylogenetic way. In addition, the two, three or even four populations presently subsumed under “*H. columbia gloveri*” (sensu lato) form, based on our barcode results, quite evidently not a genetically homogeneous population and possibly may turn out to belong to two or more different species or subspecies, in spite of only rather minor differences in the barcode sequences.

TAXONOMIC AND NOMENCLATURAL NOTES ON SOME TAXA

During our studies we found a few taxonomic and nomenclatural details regarding *Hyalophora* and some of its subordinate taxa to be either unclear or erroneous in other literature sources, which we correct here:

1. *Hyalophora* Duncan, 1841 (in Jardine [ed.], Naturalist's Library, vol. 32 = Entomology vol. 7, Exotic Moths, p. 124, 132, pl. XI); In Fletcher & Nye (1982) and Beccaloni *et al.* (2005/2014) the authorship for this taxon is given as “Duncan [& Westwood]”; however, these authors do not provide a source for their



Figures 7–10: Drawings of ♂ genitalia, *Hyalophora* species for comparison. **7.** *H. mexicana* sp. n., paratype, Zacatecas, GP no. WAN 1965/05, barcode B3218-wn-B09, UAG. **7a.** lateral view, phallus lateral view. **7b.** ventral view, phallus dorsal view. **8.** *H. euryalus*, GP no. WAN 1962/05, SMFL. **8a.** lateral view. **8b.** ventral view. **9.** *H. c. gloveri* "a" (Arizona), GP no. WAN 1963/05, SMFL. **9a.** lateral view. **9b.** ventral view. **10.** *H. columbia*, GP no. WAN 1964/05, SMFL. **10a.** lateral view. **10b.** ventral view. Drawings by Harald Lux, Berlin. Scale bars = 1 mm.

information. As Jardine's book series "The Naturalist's Library" is, first, rather rare in libraries and, second, was published under several differing cover titles (so that in different libraries slightly differing title pages and volume counts can be found for the same contents), it was not clear to us for several years whether this interpreted coauthorship was correct. However, recent digitised scans in the Biodiversity Heritage Library (general URL: www.biodiversitylibrary.org) in the internet, an original copy of the book in the private library of Colin G. Treadaway (Limbach-Wagenschwend) and photocopies from different

university libraries in personal libraries (of U. Brosch, W. A. Nässig and S. Naumann), and further the papers by Stainton (1885) and de Joannis (1926) allow the following explanations and interpretations:

a. Within the book series' counting, this publication was included in volume 32, which corresponds to the Entomology volume 7. There was evidently a double volume counting, both for the entire book series and for the main parts like Entomology etc. However, the different copies of each book apparently had either a title-page with the full volume count or with the Entomology

Table 2. Estimates of divergence over sequence pairs between groups. The number of base substitutions per site from averaging over all sequence pairs between groups are shown. Standard error estimates are shown above the diagonal [in square brackets]. Analyses were conducted using the Maximum Composite Likelihood model (Tamura *et al.*, 2004). The rate variation among sites was modeled with a gamma distribution (shape parameter = 3). The differences in the composition bias among sequences were considered in evolutionary comparisons (Tamura & Kumar, 2002). The analysis involved 40 nucleotide sequences (= specimens) in groups of populations (= possibly species or subspecies) or species (3 species of *Callosamia* united in one group). There were a total of 658 positions (= base pairs) in the final dataset. Analyses were conducted in MEGA5 (Tamura *et al.*, 2011).

Groups/taxa	<i>Callosamia</i>	<i>H. cecropia</i>	<i>H. columbia</i>	<i>H. euryalus</i>	<i>H. gloveri</i> 'a'	<i>H. gloveri</i> 'b'	<i>H. mexicana</i>
<i>Callosamia</i>		[0.015]	[0.015]	[0.014]	[0.015]	[0.014]	[0.014]
<i>H. cecropia</i>	0.098		[0.004]	[0.005]	[0.005]	[0.005]	[0.006]
<i>H. columbia</i>	0.098	0.013		[0.004]	[0.003]	[0.005]	[0.006]
<i>H. euryalus</i>	0.092	0.016	0.017		[0.005]	[0.005]	[0.006]
<i>H. gloveri</i> 'a'	0.098	0.017	0.009	0.019		[0.006]	[0.007]
<i>H. gloveri</i> 'b'	0.096	0.016	0.019	0.017	0.023		[0.006]
<i>H. mexicana</i>	0.095	0.023	0.026	0.025	0.026	0.022	

volume count only; we did not see any copy with both title pages combined thus far. The volume count as provided by Fletcher & Nye (1982) and Beccaloni *et al.* (2014) as being "vol. 33", however, does in any case not appear to be correct; at least we did not find any copy of the book with an imprint of this volume number. Also, the Entomology volume count for the "Exotic Moths" as being "vol. 5", as shown in the general page of the "Naturalist's Library" in the Biodiversity Heritage Library (2014), is not supported by any additional copy of the books which we have seen; we think this is an erroneous information in BHL. This view is also supported by Westwood's letter cited by Stainton (1885).

b. Duncan regularly uses some sort of a plural "royal we" (or "*pluralis majestatis*") instead of "I" or "the author" throughout his text. This is probably just a matter of personal style, and possibly it might also have been intended to show that Duncan agreed with publications of other authors (which were sometimes referred to in short in text or footnotes), or similarly. On p. 124, where the name *Hyalophora* was introduced for the first time and its meaning in ancient Greek was explained, Duncan wrote: "... we would assign the name *Hyalophora* ..."; this page 124 should, therefore, be taken as the original description of the generic name, not p. 132. On p. 132, the text of the different species assigned by Duncan to his genus *Hyalophora* starts with *H. cecropia*. — However, this general use of the plural "we" by Duncan alone does surely not allow to interpret a coauthorship by Duncan & Westwood for *Hyalophora*.

c. Stainton (1885), based on some correspondence in letters between him and A.G. Butler as well as J.O. Westwood, clearly showed that indeed a few parts of the text in the general introduction of the series and in some of the Entomology volumes were evidently based on Westwood's results, while most others were not, with Westwood himself even correcting some of Butler's interpretations.

Butler wrote in Stainton (1885: 181), mainly regarding "*Scopelodes unicolor*, Westwood" (see Duncan, 1841: 222): "From an examination of the text in the volume it is evident that Duncan was supplied by Westwood with the greater part of his information, and there is every reason to believe that the characters of the new genera and species were also obtained from the same source: at page 209 you will see: '*Asthenia podaliraria*, Westwood. In supplying us with a figure of this new species, Mr. Westwood has suggested the propriety of referring it, along with several others, to a new genus, which he names *Asthenia*.' Then follow the generic characters. The style of description corresponds entirely with Westwood's descriptive work. See 'Cabinet of Oriental Entomology' and other early works by this

author. At the same time, perhaps, the question is worth ventilating; Professor Westwood probably will remember whether he wrote the descriptions for Duncan or not." However, this text by Butler is evidently only concerning two taxa in which the headline of a taxon is closed with the explicit authorship "Westwood", as for example the above cited *Asthenia* or *Scopelodes*, and a few more.

In contrast, Westwood himself clearly wrote (in Stainton 1885: 183) that in cases where he provided the drawings on the plates he also included a description: "... the drawings, with a popular description of each species (not, however, accompanied by a technical Latin character) were forwarded by me to Edinburgh, but, unfortunately, I never saw a proof either of the plates which contained my figures or of the text in which my descriptions were introduced by Mr. Duncan, without any indication of what was mine or what his own comments." Thus, although Westwood did provide some of the plates printed in Entomology vol. 7, he did clearly not produce pl. XI of vol. Entomology 7 illustrating *Hyalophora cecropia*. Therefore, any coauthorship by Westwood for *Hyalophora* cannot be interpreted from the painting, following Westwood's personal comment in Stainton (1885: 183, 185–186).

The same result (Duncan as sole author for *Hyalophora*) was also achieved by de Joannis (1926: 10), however, with an incorrect type species interpretation.

Summarised: There does not appear any reason whatsoever to interpret a combined authorship "Duncan [& Westwood]" specifically for the genus *Hyalophora*. — For any other new taxa introduced in the Entomology volume 7 of Jardine's Naturalist's Library and as well for Entomology vols. 1 and 6, only a critical reading of both Duncan's and Stainton's texts can reveal the correct authorships; a generalised "Duncan [& Westwood]" for all new taxa is surely incorrect. Westwood was, by his own statement in Stainton (1885: 182), explicitly not general coauthor for vols. Entomology 2–5.

Regarding the type species fixation for the genus *Hyalophora* (i.e., *Phalaena cecropia* Linnaeus, 1758, by subsequent designation by Grote, 1865: 227) we follow Fletcher & Nye (1982: 79–80), who summarised the different interpretations by several authors, including Ferguson (1972: 245). Grote's earlier paper of the same year 1865, cited by Fletcher & Nye (1982), was not available to us; presently these earliest issues of the "Practical Entomologist" of 1865 are not available, neither in German libraries nor in form of digitised scan PDFs in the internet. Accepting the evidently well-argued interpretation of Fletcher & Nye (1982), however, supports stability of nomenclature.



Figure 11. Mexico, Zacatecas. Collecting locality of *Hyalophora mexicana*.

2. *H. c. nokomis* (Brodie, 1894): In Beccaloni *et al.* (2014), the publication of Brodie is cited to be published in 1884. However, the reprint of this paper by Riotte (1970) clearly indicates an original publication date in 1894, just as well as Ferguson (1972). In earlier years we did not have access to any original copy of this very rare Canadian publication series “The Biological Review of Ontario” (and thus based our interpretation in the beginning solely on the reprint by Riotte, 1970), but in the meanwhile, since 2012, a scan PDF of this publication is available in the Biodiversity Heritage Library. So we can finally solve the question here now: the short paper by Brodie was indeed published in October 1894. — We suggest this might just have been a simple typing error in the BMNH Card Index.

3. *H. c. kasloensis* Cockerell [*in Packard*], 1914: This taxon is listed in error as “*kasloensis* Cockerell, 1908” by Beccaloni *et al.* (2014). This cited earlier paper of “Cockerell (1908)” was, in fact, written by J.W. Cockle (not by T.D. Cockerell) and does not contain a formal description of a new taxon, but only a short note and morphological description without naming of what six years later was then described by Cockerell [*in Packard*] (1914: 226, footnote) as *kasloensis*. — This was evidently a combined double error: first, by a misspelling (Cockerell instead of Cockle) while writing by hand the earlier citation onto the card “*kasloensis*” of the BMNH Card Index, but with the correct statement “as *rubra*” (i.e., without a remark on any original description), and, second, by a misinterpretation of this handwritten note while transferring the card contents into the digital Global Lepidoptera Names Index. The error may have been supported by the slightly ambivalent text by Cockerell *in Packard* (1914).

ACKNOWLEDGEMENTS

Several colleagues helped us during preparation of the present manuscript: Michael M. Collins, Daniel Herbin, Carlos C.G. Mielke, John Rawlins, and Rodolphe Rougerie provided material, information and/or sequence data and/or discussed parts of the manuscript with the authors. Ulrich Brosch, Richard S. (Ric) Peigler and Colin G. Treadaway provided literature references and loaned or copied old and rare publications. One of the authors (G.N.G.) acknowledges the support by his son Guillermo Nogueira L. during many of his collecting trips helping during day and night. Harald Lux kindly produced the genitalia drawings; the genitalia in Fig. 6 were scanned by Wolfgang Eckweiler. Michael M. Collins and a second, anonymous reviewer as well as the editor, Konrad Fiedler, helped us to improve the manuscript.

Our molecular work was mainly funded by NSERC and Genome Canada through grants to Paul D. N. Hebert at the Canadian Centre for DNA Barcoding based at the Biodiversity Institute of Ontario at the University of Guelph, Ontario, Canada, until mid-2012.

EDITOR’S NOTE

The electronic edition of this article has been registered in ZooBank to comply with the requirements of the amended International Code of Zoological Nomenclature (ICZN). This registration makes this work available from its electronic edition. ZooBank is the official registry of Zoological Nomenclature

according to the ICZN and works with Life Science Identifiers (LSIDs). The LSID for this article is: urn:lsid:zoobank.org:pub:6D66A3E0-FE85-43E1-A4F3-26C473C641F4. Registration date: October 28th, 2014. This record can be viewed using any standard web browser by clicking on the LSID above.

LITERATURE CITED

- BOLD [OR BARCODE OF LIFE OR BOLDSYSTEMS]. 2014. [BOLD platform, version 3.6]. URL: www.barcodinglife.org or www.boldsystems.org. Last accessed: 2014-08-14.
- BECCALONI, G., M. SCOBLE, I. J. KITCHING, T. SIMONSEN, G. S. ROBINSON, B. PITKIN, A. HINE & C. LYAL. 2005/2014. The Global Lepidoptera Names Index. URL: www.nhm.ac.uk/research-curation/research/projects/lepindex/. Database last updated Feb. 2005, last accessed: 2014-08-05.
- BEUTELSPACHER BAIGTS, C. R. & M. A. BALCÁZAR LARA. 1994. Catálogo de la familia Saturniidae de México. Tropical Lepidoptera 5, Supplement 1: 1–28.
- BIODIVERSITY HERITAGE LIBRARY. 2014. The Naturalist's Library. URL: www.biodiversitylibrary.org/bibliography/17346#/summary, last accessed: 2014-08-12.
- BOISDUVAL, J. B. A. DE. 1855. [Séance du 28 Mars 1855: No title, notes on insects of California, with description of *Saturnia euryalus*.] Bulletin de la Société entomologique de France [= Proceedings of the meetings of the society], 1855, premier trimestre, pp. xxxi–xxxii. [Published together with Annales de la Société entomologique de France, sér. 3, tome 3.]
- BRODIE, W. 1894. *Platysamia columbia nokomis*. The Biological Review of Ontario 1(4): 103–107.
- CCDB [CANADIAN CENTRE FOR DNA BARCODING]. 2014. URL: ccdb.ca/ [technical protocols: ccdb.ca/resources.php]. Last accessed: 2014-08-12.
- COCKLE, J. W. 1908. *Samia rubra*. [Note on a population of *Hyalophora euryalus* from Brit. Columbia, Canada; without description.] Entomological News 1908: 340–341.
- COLLINS, M. 1984. Genetics and ecology of a hybrid zone in *Hyalophora*. University of California Press, Series in Entomology 104: 1–93.
- COLLINS, M. M. 1997. Hybridization and speciation in *Hyalophora* (Insecta: Lepidoptera: Saturniidae): A reappraisal of W. R. Swadner's classic study of a hybrid zone. Annals of the Carnegie Museum 66(4): 411–455.
- COLLINS, M. 2007. Mothcatcher: An evolutionist's journey through canyon and pass. Reno/Las Vegas (University of Nevada Press), [xx] + 176 pp.
- COLLINS, M. M. & J. E. RAWLINS. 2014 ["2013"]. A transect for reproductive compatibility and evidence for a "hybrid sink" in a hybrid zone of *Hyalophora* (Insecta: Lepidoptera: Saturniidae). Annals of the Carnegie Museum 82(2): 193–223.
- DECAËNS, T. & R. ROUGERIE. 2008. Descriptions of two new species of Hemileucinae (Lepidoptera: Saturniidae) from the region of Muzo in Colombia: evidence from morphology and DNA barcodes. Zootaxa 1944: 34–52.
- DE JOANNIS, J. 1926. Westwood ou Duncan. Annales de la Société entomologique de France 95(1): 1–11.
- DUNCAN, J. [PARTIM: & J. O. WESTWOOD]. 1841. Entomology vol. VII. Exotic moths. In: Jardine, W. (ed.), The Naturalist's Library, vol. XXXII. Edinburgh (W. H. Lizars).
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39(4): 783–791.
- FERGUSON, D. C. 1972. Fascicle 20.2B, Bombycoidea, Saturniidae comprising subfamilies Hemileucinae (conclusion), Saturniinae. Pp. 155–275, xv–xxi, pls. 12–22 in: R. B. Dominick, C. R. Edwards, D. C. Ferguson, J. G. Franclemont, R. W. Hodges & E. G. Munroe (eds.), The moths of America north of Mexico including Greenland. London (E. W. Classey, R. B. D. Publ.).
- FLETCHER, D. S. & I. W. B. NYE. 1982. Bombycoidea, Castnioidea, Cossioidea, Mimallonoidea, Sesiioidea, Sphingoidea, Zygaenoidea. In: Nye, I. W. B. (ed.), The generic names of moths of the world, vol. 4. London (Trustees of the BMNH), 1 pl., xiv + 192 pp.
- GARCIA, E. 1973. Modificaciones al sistema de clasificación climática de Köppen (para adaptarlo a las condiciones de la República Mexicana). México D.F. (Universidad Nacional Autónoma de México), 146 pp.
- GARCIA-MENDOZA, A. J., M. J. ORDOÑEZ & M. BRIONES-SALAS. 2004. Biodiversidad de Oaxaca. México D.F. (Instituto de Biología UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, World Wildlife Fund, ed. Redacta), pp. 107–115, 145–162, 219–225.
- GONZÁLEZ, V. L. M. 1986. Contribución al conocimiento del género *Quercus* (Fagaceae) en el Estado de Jalisco. Guadalajara, Jalisco (Colección Flora de Jalisco, Instituto de Botánica, Universidad de Guadalajara), 240 pp.
- GROTE, A. R. 1865. Notes on the Bombycidae of Cuba [footnote on pp. 227–228]. Proceedings of the Entomological Society of Philadelphia 5: 227–255.
- HOFFMANN, C. C. 1942. Catálogo sistemático y zoogeográfico de los Lepidópteros Mexicanos, Tercera parte, Sphingoidea y Saturnioidea. Anales del Instituto de Biología, Universidad Nacional de México 13(1): 213–256 [reprinted 1976 by Sociedad Mexicana de Lepidopterología].
- INEGI. 1981a. Carta Geológica (Guadalajara) [geological map of Guadalajara]. México D.F. (Secretaría de Programación y Presupuesto ed.).
- INEGI. 1981b. Carta Geológica (México) [geological map of Mexico]. México D.F. (Secretaría de Programación y Presupuesto ed.).
- KOHALMI, L. & P. MOENS. 1975. Evidence for the existence of an intergrade population between *H. gloveri nokomis* and *H. columbia* in northwestern Ontario. Canadian Entomologist 107: 793–799.
- KOHALMI, L. & P. MOENS. 1988. Pattern of inheritance of larval tubercle-colour polymorphism in *H. columbia* of northwestern Ontario. Genome 30: 307–312.
- LAMPE, R. E. J. 2010. Saturniidae of the world, their lifestages from the eggs to the adults — Pfauenspinner der Erde, ihre Entwicklungsstadien vom Ei zum Falter. München (F. Pfeil), 368 pp. incl. 336 col. pls.
- LEMAIRE, C. 1978. Les Attacidae Américains, The Attacidae of America (= Saturniidae), 1. Attacinae. Neuilly-sur-Seine (ed. C. Lemaire); 239 pp., 49 pls.
- LEMAIRE, C. 1996. 117. Saturniidae. Pp. 28–49 in: Heppner, J. B. (ed.), Atlas of Neotropical Lepidoptera. Checklist: Part 4B. Drepanioidea, Bombycoidea, Sphingoidea. Gainesville (Association for Tropical Lepidoptera).
- LINNAEUS, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiae, 822 pp. [+ 5 pp. without pagination].
- LLORENTE, B. J., A. A. N. GARCÍA & S. E. GONZÁLEZ. (1996). Biodiversidad taxonómica y biogeográfica de Artrópodos de México. México D.F. (Universidad Autónoma de México ed.), 660 pp.
- MARTÍNEZ, M. 1948. Los Pinos Mexicanos. México D.F. (Ediciones Botas), 361 pp.
- MARTÍNEZ, M. 1991. Catálogo de nombres vulgares y científicos de plantas mexicanas. México D.F. (Fondo de Cultura Económica ed.), 1247 pp.
- MARTÍNEZ-CRUZ, J., O. TÉLLEZ VALDÉZ & G. IBARRA-MANRIQUEZ. 2009. Estructura de los encinares de la Sierra de Santa Rosa, Guanajuato, México. Revista Mexicana de Biodiversidad 80(1): 145–156.

- NÄSSIG, W. A., S. NAUMANN, & R. ROUGERIE. 2010. Evidence for the existence of three species in the genus *Archaoattacus* (Lepidoptera: Saturniidae). *Journal of Research on the Lepidoptera* 43: 37–47.
- NAUMANN, S. & S. LÖFFLER. 2013. Two new species of the genus *Cricula* Walker, 1855 from Myanmar and India, with synonymic notes (Lepidoptera: Saturniidae). *Nachrichten des Entomologischen Vereins Apollo N.F.* 33(4): 177–184.
- NEI, M. & S. KUMAR. 2000. *Molecular evolution and phylogenetics*. New York (Oxford Univ. Pr.), 348 pp.
- PACKARD, A. S. [POSTHUMOUSLY EDITED BY T. D. COCKERELL]. 1914. *Monograph of the bombycine moths of North America, including their transformations and origin of the larval markings and armature. Part III, Families Ceratocampidae (exclusive of Ceratocampinae), Saturniidae, Hemileucidae, and Brahmaeidae*. *Memoirs of the National Academy of Sciences*, 12 (1, 1): [ix] + 516 pp. [incl. CXIII pls.].
- PEIGLER, R. S. 1994. Non-sericultural uses of moth cocoons in diverse cultures. *Proceedings of the Denver Museum of Natural History, Series 3*, 5: 1–20.
- PEIGLER, R. S. & P. A. OPLER. 1993. *Moths of Western North America. I. Distribution of Saturniidae of Western North America*. Fort Collins (C. P. Gillette Insect Biodiversity Museum, Dept. of Entomology, Colorado State University), 24 unnumbered pp.
- POWELL, J. A. & P. A. OPLER. 2009. *Moths of western North America*. Berkeley, Los Angeles, London (University of California Press), xiii + 369 pp., 64 col. pls. with legends.
- RATNASINGHAM, S. & P. D. N. HEBERT. 2007. Barcoding. BOLD: The barcode of life data system (www.barcodinglife.org). *Molecular Ecology Notes* 7(3): 355–364.
- RIOTTE, J. C. E. 1970. A contribution to the knowledge of *Hyalophora* (*Hyalophora*) *columbia* (Lep.: Saturniidae) [containing a reprint of Brodie 1894]. Toronto Entomologists' Association, Occasional Publications no. 2, [1] + 5 pp.
- RZEDOWSKI, J. 1994. *Vegetación de México*. México (D.F.) (Limusa-Noriega Editores), 432 pp.
- SAITOU, N. & M. NEI. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology & Evolution* 4(4): 406–425.
- SMITH, M. J. & R. E. WELLS. 1993. Rediscovery of *Hylophora euryalus cedrosensis* (Saturniidae), with descriptions of the adult and larval stages. *Journal of the Lepidopterists' Society* 47(2): 114–124.
- SMITH, S. I. 1865. Description of a species of *Samia*, supposed to be new, from Norway, Me [= Maine]. *Proceedings of the Boston Society of Natural History* 9 (for 1862/63): 342–345.
- STANTON, H. T. 1885. On the authorship of the letter-press in volumes I, VI, and VII of the *Entomology* in "Jardine's Naturalist's Library". *The Entomologist's Monthly Magazine* 21: 181–186.
- STRECKER, F. H. H. 1872–1877. *Lepidoptera Rhopaloceres and Heteroceres indigenous and exotic with descriptions and colored illustrations*. Reading (Owens's Stream Book and Job Printing Office), 143 pp., col. pls. I–XV.
- SWEADNER, W. R. 1937. Hybridization and the phylogeny of the genus *Platysamia*. *Annals of the Carnegie Museum* 25: 163–242.
- TAMURA, K. & S. KUMAR. 2002. Evolutionary distance estimation under heterogeneous substitution pattern among lineages. *Molecular Biology & Evolution* 19(10): 1727–1736.
- TAMURA, K., M. NEI & S. KUMAR. 2004. Prospects for inferring very large phylogenies by using the neighbor-joining method. *Proceedings of the National Academy of Sciences USA* 101(30): 11030–11035.
- TAMURA, K., D. PETERSON, N. PETERSON, G. STECHER, M. NEI & S. KUMAR. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology & Evolution* 28(10): 2731–2739.
- TUSKES, P. M., J. P. TUTTLE & M. M. COLLINS. 1996. *The wild silk moths of North America. A natural history of the Saturniidae of the United States and Canada*. Ithaca, London (Comstock, Cornell); i–xi + 250 pp., 30 pls.
- TUTTLE, J. P. 1985. Maintaining species integrity between sympatric populations of *Hyalophora cecropia* and *Hyalophora columbia* (Saturniidae) in central Michigan. *Journal of the Lepidopterists' Society*, 39(2): 65–84.
- VAGLIA, T., J. HAXAIRE, I. J. KITCHING, I. MEUSNIER & R. ROUGERIE. (2008). Morphology and DNA barcoding reveal three cryptic species within the *Xylophanes neoptolemus* and *loelia* species-groups (Lepidoptera: Sphingidae). *Zootaxa* 1923: 18–36.
- VAZQUEZ-GARCIA, J. A., M. J. CHAZARO, H. G. NIEVES, Y. L. VARGAS-RODRIGUEZ, G. M. VAZQUEZ & M. A. FLORES. 2004. *Flora del Norte de Jalisco y Etnobotánica Huichola*. Guadalajara, Jalisco, México (Serie Fronteras de Biodiversidad, Universidad de Guadalajara, CUCBA-CUCSH ed.), 182 pp.
- ZAVALA, C. F. 2003. *Identificación de encinos de México*. Texcoco, Edo. de México (Universidad Autónoma Chapingo ed.), 190 pp.
- ZWICK, A. 2009. The principal structure of male genital sclerites and muscles of bombycoid moths, with special reference to Anthelidae (Lepidoptera: Bombycoidea). *Arthropod Structure & Development* 38: 147–161.